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RESEARCH ARTICLE

Chilling to the bone: Lower temperatures increase vertebrate predation by *Tonatia bidens* (Chiroptera: Phyllostomidae)

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ABSTRACT. The greater round-eared bat, *Tonatia bidens* (Spix, 1823), is a medium-sized phyllostomid bat distributed in the north of Argentina, Paraguay and Brazil. The diet and foraging patterns of this species are poorly known. We analyzed the composition of the diet of a population of *T. bidens* and how the temperature influences the consumption of vertebrates and invertebrates. To describe diet composition, we conducted weekly collections of food scrap from two monospecific night-perches. Data of temperature for the study period were taken from the meteorological station installed 300 m from the collection perches. The influence of temperature was evaluated using generalized linear models (GLMs) with negative binomial distribution. *Tonatia bidens* consumed 28 taxons (204 records), being at least 17 Artropods and 11 Passeriformes birds. Temperature explained a greater proportion of vertebrate abundance ($R^2 = 0.23$) than invertebrate ($R^2 = 0.16$) or to both pooled ($R^2 = 0.11$). The relation with temperature was positive with invertebrates and negative with the vertebrates. The diet of the population of *T. bidens* comprised mainly invertebrates, which were the most frequent and diverse taxa. Data suggests that *T. bidens* has a diverse diet, with proportion of the item's consumption varying temporally. Environmental factors, such as the temperature presented on this work, seems to be good proxies for the dietary traits of this species.

KEY WORDS. Atlantic Forest, bat diet, diet seasonality, invertebrate predation, trophic guild.

INTRODUCTION

The greater round-eared bat *Tonatia bidens* (Spix, 1823) is a medium size phyllostomid bat distributed in the North of Argentina, Paraguay and Brazil (Williams and Genoways 2007, Peracchi et al. 2011). Despite its wide distribution, *T. bidens* is considered rare in inventories (see Esbérard 2003, Fischer et al. 2015), which justifies its classification in the "insufficient data" category on the Red List of the International Union for Conservation of Nature – IUCN (Barquez and Díaz 2016). Individuals of *T. bidens* are usually found in open environments nearby forest fragments (Esbérard and Bergallo, 2004, Felix et al. 2013), gathering in small colonies in caves (Pinto-da-Rocha 1995), tree hollows, water mines and manillas (Martuscelli 1995, Esbérard and Bergallo 2004).

The diet of *T. bidens* is mainly composed of invertebrates from the Orders Lepidoptera, Coleoptera, Blattodea, Orthoptera and Hemiptera (Martuscelli 1995, Esbérard and Bergallo 2004, Felix et al. 2013), and of vertebrates as small birds, rodents, anurans and other bats (Baker et al. 1976, Esbérard and Bergallo 2004). In addition to the animalivorous diet, individuals also consume

fruits and leaves (Félix et al. 2013). Due to the dietary plasticity, the classification of *T. bidens* in one of the trophic guilds proposed for Neotropical bats (see Kalko 1998) is still controversial.

The diet of *T. bidens* is known only for a few localities, making it difficult to evaluate the trophic ecology of this species. In Brazil, there are records of *T. bidens* in 12 states (Peracchi et al. 2011), but information about the diet composition of the species in the Atlantic Forest biome comes of observations from only two states of southeastern Brazil (Martuscelli 1995, Esbérard and Bergallo 2004, Felix et al. 2013). Insufficient data hinders the study of temporal and spatial variations in the populations' diet, which have been described for other Phyllostomidae species, for instance *Artibeus lituratus* (Olfers, 1818) and *Sturnira lilium* (E. Geoffroy, 1810) (e.g, Passos and Graciolli 2004, Mello et al. 2004, Barros et al. 2013, Bôlla et al. 2018). Variations in diet among sexes, seasons and localities were also described for other families, as the Noctilionidae *Noctilio leporinus* (Linnaeus, 1758) (Noctilionidae), a broadly distributed animalivorous species (Bordignon 2006). These studies identified the availability of resources, environment type and temperature as the most important variables involved in the food choices by individuals of different species (Bordignon 2006).

The diet of *T. bidens* is primarily based on small living animals. Since the availability of these potential resources change temporally, we hypothesize that the diet of *T. bidens* changes according to the known seasonal variations in their availability, mainly invertebrates (Hails 1982). The consumption of invertebrate may decrease on colder months and increase in warmer months and vertebrate predation, an opportunistic habit of this species, may be constant during the year. To test these hypotheses, we analyzed the influence of temperature, as a proxy of prey availability, in the diet of a *T. bidens* population in the largest continuous remnant of Atlantic Forest in Brazil.

MATERIAL AND METHODS

We sampled bats' roosts at Reserva Particular do Patrimônio Natural (RPPN) Salto Morato (25°10'27"S; 48°17'49"W), located in the Guaraqueçaba municipality, Northern coast of Paraná, southern Brazil (Fig. 1). The climate of the region, according to Köeppen's classification, is Cfa: Humid subtropical, with warm summers, no defined dry season and annual average temperature between 17 and 21 °C (Alvares et al. 2013).

The RPPN Salto Morato is part of the largest continuous remnant of the Atlantic Forest biome, which covers 22.53 km². This reserve is inserted in the Environmental Protection Area of Guaraqueçaba (APA de Guaraqueçaba – FBPN 2011) and in the Serra do Mar sub-region. The predominant forest formation is Dense Ombrophilous Forest. The annual rainfall at RNSM is 2,500 mm with monthly average of 293 mm, on average, with more intense rains from November to April (Fig. 2).

To describe the composition of the diet of *T. bidens*, we performed weekly collections of food scrap in two monospecific night-perches between March 2013 and November 2013. These

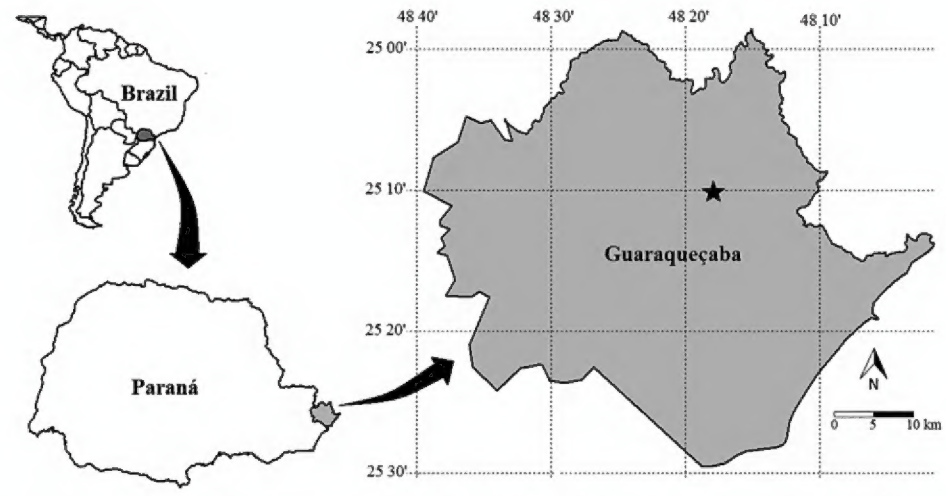

Figure 1. Localization of Reserva Particular do Patrimônio Natural (RPPN) Salto Morato (black star) in the municipality of Guaraqueçaba, northern coast of Paraná state, southern Brazil.

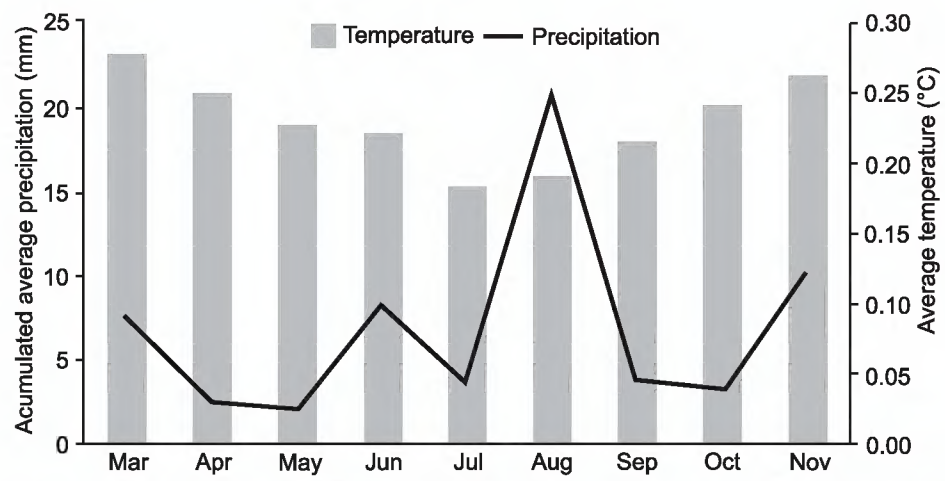

Figure 2. Variation in the precipitation and average temperature from March to November 2013, obtained in a meteorological station, installed in the RNSM area, on the northern coast of Paraná state. Samplings were carried between March 2013 and July 2014.

perches were located externally to the roof of the buildings and lodgings for visitors of the RPPN Salto Morato. In each of the perches we manually collected all food scraps left by the bats, which were allocated in plastic bags identified with month.

In the lab, samples were examined, and food items were identified to the lowest possible taxonomic level. We used the keys of Triplehorn and Johnson (2011) and Rafael et al. (2012) to identify the Arthropods, and expert consultation from the Universidade Federal do Paraná to identify Lepidoptera. We identified birds based on the identification guides of Souza (2004) and Sigrist (2009), and expert consultation. Data on temperature for the study period were taken from the meteorological station installed in the RPPN, which is located at 300 m from the collection perches. We did not capture or handle bats and bats' food scraps were sampled under SISBIO license (process 36103-3).

The food items of *T. bidens* were described according to the richness and frequency of the food items, and the number of items. We considered the total number of taxons observed in each sample (pool of four weekly collections) as a measure of richness for each sampled month. We categorized the items frequency according to the Constancy Index (C), which separates the frequency (number of samples of the studied taxon divided by the total

number of samples) into three categories: Rare – less than 25%, Uncommon – from 26% to 50% and, Frequent – present in more than 50% of the samples. To determine the number of the items (abundancy) we used the protocol described by Felix et al. (2013).

The influence of temperature on the food items consumed by *T. bidens* was evaluated using generalized linear models (GLMs) with negative binomial distribution due to the over dispersion of the data. For the analyses, the response variables were number of records of: invertebrates ("abundance of invertebrates" from now on), vertebrates ("abundance of vertebrates" from now on) or vertebrates and invertebrates pooled ("total abundance" from now on). We used monthly temperature averages as a predictor variable. All analyses were performed in the software R version 3.4.2, using the "MASS" package.

RESULTS

Tonatia bidens consumed specimens of 28 taxons (204 records), at least 17 of which were Artropods and 11 were Passeriform birds (Table 1). Among these taxons, 42.9% were classified as "Rare", 32.1% as "Uncommon" and 25% as "Frequent". Among the monthly samples, for the vertebrates, the Passeriformes (55.6%), Trochilidae (44.4%), *Troglodytes musculus* Naumann, 1823, *Thalurania glaucopis* (Gmelin, 1788) and Apodiform (with 33.3% each) were the most frequent items (Table 1). Among the Artropods, the Blattidae (88.9%), Tettigoniidae (77.8%) and Cerambycidae (66.7%) were the most frequent consumed families (Table 1).

Temperature explained a greater proportion of vertebrate abundance variation ($R^2 = 0.23$) than invertebrate ($R^2 = 0.16$) or both pooled ($R^2 = 0.11$), and the relationship of temperature with invertebrates was positive, being negative with vertebrates (Fig. 3).

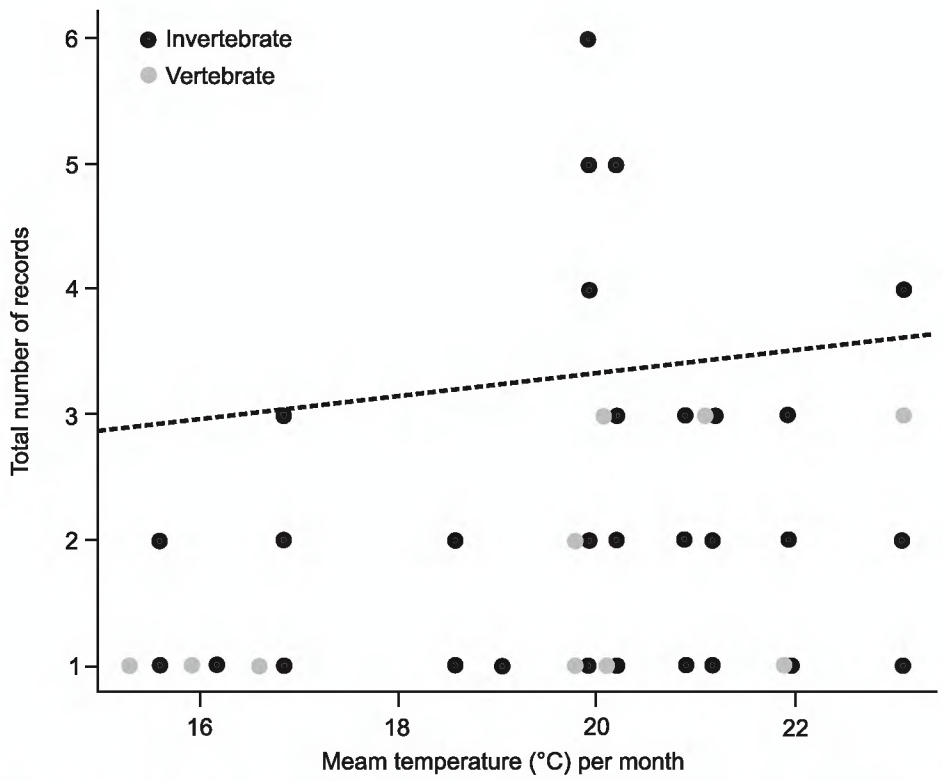

Figure 3. Relation of mean temperature (°C) per month and the number of records of invertebrate (black dots) and vertebrates (grey dots). Dashed line represents the vertebrate model.

Table 1. List of taxons, monthly abundance, total (AB) and frequency (FR) of the occurrence of the items consumed by *Tonatia bidens* in Atlantic Forest environment, in northern coast of Paraná State, southern of Brazil.

Taxons	Sampling months									AB	FR
	M	A	M	J	J	A	S	O	N		
Vertebrates											
Passeriformes											
Onychorhynchidae											
Myiobius sp.					1					1	11.1
Parulidae											
Basileuterus culicivorus			1							1	11.1
Rhynchocyclidae											
Leptopogona maurocephalus			1							1	11.1
Phylloscartes oustaleti					1					1	11.1
Rhynchocyclidae											
Rhynchocyclidae sp.				2	1					3	22.2
Thraupidae											
Tangara seledon				1	1					2	22.2
Troglodytidae											
Troglodytes musculus	2	1			1					4	33.3
Passeriformes sp.	1		1		1	1			1	5	55.6
Apodiformes											
Apodiformes sp.						2	1	1		4	33.3
Trochilidae											
Thalurania glaucopis			1	1	1					3	33.3
Trochilidae sp.		1			1	1	1			4	44.4
Invertebrates											
Blattodea											
Blattidae	3	6	2	1		1	1	1	1	16	88.9
Blattodea sp.	2		2		1					5	33.3
Coleoptera											
Cerambycidae	4	3	1		3			3	2	16	66.7
Scarabaeidae	1				1			1		3	33.3
Coleoptera sp.	8	3	5	1			1	5		23	66.7
Hemiptera											
Cicadidae	2	2						1		5	33.3
Hemiptera sp.									1	1	11.1
Lepidoptera											
Erebidae		1			1		1			3	33.3
Geometridae		1								1	11.1
Hepialidae	1					1				2	22.2
Noctuidae		2								2	11.1
Nymphalidae			1		1					2	22.2
Sphingidae	2	8	8				6			24	44.4
Lepidoptera sp.	3	4	2	1	5	1	1	2		19	88.9
Orthoptera											
Gryllidae		3								3	11.1
Tettigoniidae	5	5	7	1	1	1	3			23	77.8
Orthoptera sp.	8	7	1	1	2	1	1	4	2	27	100
Total records	42	47	33	9	23	9	16	18	7	204	

DISCUSSION

The population of *T. bidens* analyzed consumed mainly invertebrates, which were the most frequent and diverse taxons. Contrary to our hypothesis, temperature explained the consumption of vertebrates better than the consumption of invertebrates, even though there was a greater consumption of Arthropods between May and August. This latter pattern can be due to the lower abundance of Arthropods on cold periods (Hails 1982), what would force individuals feed more on vertebrates. These results corroborate other studies in the Brazilian Southeast, which showed that the consumption of leaves and vertebrates increases in drier months, when many Arthropods go on diapause (Felix et al. 2013). Our results indicate that, besides environmental variation, the diet of *T. bidens* varies seasonally, at least in the southeastern and southern Brazil.

Cockroaches were consumed in greater numbers among the invertebrate, when compared with moths and beetles. This is inconsistent with the other studies' results, which found that Coleoptera and Lepidoptera were the most frequently consumed items in *T. bidens* diet (see Felix et al. 2013, Esbérard and Bergallo 2004). This difference may indicate that the composition of this species diet varies throughout its distribution, and probably changes according to the environment. Although there is little information in literature about the diet of *T. bidens* in other areas, hindering comparison, there are records for other bat species (see Bôlla et al. 2018), including animalivores species (see Bordignon 2006). Even though geographical variation may be important for *T. bidens* diet, this hypothesis still needs to be tested.

The high richness (41% of all the taxons consumed) and frequency of occurrence (at least a record in each sample) of birds in the diet of *T. bidens* indicates that this food item is an important resource for the species. In other areas of Atlantic Forest, *T. bidens* was recorded preying on 75 individuals of 28 bird species (Martuscelli 1995), mainly medium-sized species – average weight 13.5 g (Del Hoyo et al. 2018, average calculated by the authors based on bird records in literature and in our data).

Data obtained in the South and Southeast portions of the Atlantic Forest suggest that the diet of *T. bidens* varies temporally (e.g., Passos and Graciolli 2004, Mello et al. 2004). The reasons for this variation are still poorly understood. Environmental factors such as the temperature could be 'proxies' for the biological and physiological aspects of the species (e.g., reproductive season). In low temperatures (about 14 °C), lactating females, for example, can have their metabolic rate increased by 200% to keep their body temperatures and insectivorous females may increase their arthropod ingestion by about 22% during pregnancy (Neuweiler 2000: 255–256). Reproductive processes may increase energetic demands and thus influence the kind of food item or the amount of food ingested (Neuweiler 2000). The reliance of *T. bidens* on vertebrates may be a more advantageous strategy than increasing invertebrate consumption during cold months.

Based on the results of our work and on other studies on the species, we suggest that *T. bidens* is embedded in the Omnivores guild, since guild classifications do not account for seasonal variations and a more general classification (such as omnivorous) solves the disagreement among the previous trophic classifications (e.g., Goodwin and Greenhall 1961, Myers and Wetzel 1983).

As observed for other Neotropical bats, the knowledge about the ecological and biological attributes of *T. bidens* is limited, which classifies this species as "insufficient data" on endangered species' lists (Barquez e Díaz 2016). In the state of Paraná, more specifically, this species is included in the Conservation Plan for Threatened Mammal Species (Plano de Conservação para Espécies de Mamíferos Ameaçados, in Portuguese) which indicated the necessity of studies on its biology and ecology (Miranda et al. 2009). Even though occasional studies on the composition of the bats' diet are fundamental to understand the needs of different species, it is also important to identify possible temporal variations in the use of food resources and how it affects the habitat choice by the organisms, particularly in the case of rare species like *T. bidens*.

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